

Postnatal physical and behavioural development of *Praomys* (*Mastomys*) *natalensis* (A. Smith, 1834)

By C. M. BAKER and J. MEESTER

From the Department of Zoology, University of Natal, Pietermaritzburg

Receipt of Ms. 1. 2. 1977

Introduction

This study describes the growth and behavioural development of *Praomys* (*Mastomys*) *natalensis* (A. Smith, 1834) during the first six weeks of life, under laboratory conditions. Although previous workers (OLIFF 1953; JOHNSTON and OLIFF 1954; MEESTER 1960; MEESTER and HALLETT 1970) have studied reproduction and postnatal development in *P. natalensis*, few detailed behavioural observations have been recorded. An attempt is made to describe the behavioural development during the natural periods described by WILLIAMS and SCOTT (1953). These are based on important changes that occur during growth, and indicate critical stages in the development of social behaviour patterns.

Materials and methods

The animals here reported on were derived from specimens trapped during March 1976 near Baynesfield railway station, Pietermaritzburg. They were maintained in pairs in 42×25×22 cm cages, and were fed on standard mouse pellets and water. Paper waste and wood shavings were used as nesting material.

The young (10 litters) were all born in captivity, mainly from captive matings. Their day of birth is referred to as day 0. Observations were carried out once a day (in the evenings) for the first 20 days and then every other day until the litter reached 40 days of age.

During the observation periods the average mass of each litter was recorded, as well as mean head and body length, tail, hind-foot and ear lengths (Fig. 1 and 2). From the 20th day onwards the young were anaesthetized with ether in order to obtain these data.

Behavioural development was determined by observing each litter in its cage and by using the following experimental methods (BROOKS 1972):

1. Righting: The animal is placed on its back on a flat surface, and its ability to right itself is noted.
2. Cliff-drop aversion: The animal is placed on an elevated box, 7.5 cm high. Cliff-drop aversion is shown by moving away from the edge.
3. Negative geotaxis: The animal is placed facing down a slope at an angle of 45°. Negative geotaxis is indicated by turning and moving up the slope.
4. Clinging ability: The animal is placed on a 0.5 cm wide bar, 5.5 cm high. Its ability to cling to and to walk along the bar is noted.
5. Contact: All the young from one litter are placed in a group. Contactual urge is shown by the tendency of the young to group together. A tendency to break away from this group indicates the development of exploratory behaviour.
6. Isolation: All the young from one litter are placed at equal distances (10 cm) apart.

Posture as well as any vocalizations and motor responses are recorded.

To obtain an indication of the gonadal development of the young, the testes and ovaries were removed from three males and three females at the following intervals: a) 5 days; b) 10 days; c) 15 days; d) 20 days; e) 25 days; f) 30 days and g) 40 days.

The tissues were fixed with Bouin's fluid and stored in 70 % alcohol. Paraffin wax was used for embedding, and all sections were stained in haematoxylin and eosin. An indication of testis development was obtained by measuring seminiferous tubule diameter, and of ovary development by noting the occurrence of Graafian follicles.

The information obtained from these sections was used in an attempt to correlate physiological development with the development of sexual behaviour patterns.

Observations

Litter size and sex ratio

Data were obtained from 11 litters varying in size from eight to 17 young, with $\bar{x} = 11,27$, and $SD = 2,28$. This was somewhat higher than was found by MEESTER (1960), who gave \bar{x} as 8,53, with $S.D. = 3,91$. This difference is significant at the 5 per cent level ($t = 2,40$, 18 degrees of freedom; $0,05 > P > 0,02$). The single litter of 17 young was killed by the parents on day 1. The sex ratio of the remaining young at birth was 49 ♂♂ : 55 ♀♀. This does not differ significantly from a 1:1 ratio ($X^2 = 0,24$; $0,7 > P > 0,5$). The shortest interval between litters was 29 days (litters 3 and 5).

Mean mass and growth data are summarized in figures 1 and 2. Mass increase was greatest from birth until day 5 (fig. 1). Between the 38th and 40th days no increase was noted. Hind foot and ear length showed a similar initial period of rapid increase. Head-body and tail lengths experienced a more linear increase, the growth curves becoming flatter only from the 20th day onwards (Fig. 2).

Physical development

General appearance at birth was similar to that noted by MEESTER (1960). The limbs, tail, nose and crown of the head were translucent pink in colour, the remainder of the body having a grey tinge. Corresponding to the mid-dorsal unpigmented zone described by MEESTER (1960) was a 'groove'. The belly skin was transparent, allowing the organs within to be seen. In all cases the umbilical cord had been bitten off very close to the belly surface by the mother.

On the second day a grey tinge began to appear on the tail, limbs and closed ear flaps. The mid-dorsal line began to appear in the head region, and corresponded to the unpigmented 'groove' noted at birth. This line slowly spread along the dorsal midline and then gradually faded out from the 13th day onwards.

The young were born with short, sparse hair approximately 2 mm in length. From the eighth day short, soft and dense hair began to appear, which grew to form the adult pelage. The spikier juvenile hair remained until the end of the observation period (40 days) but was absent from mature adults. At birth the tails of the young were naked, but from the second day short, spiky hair began to appear. In most of the young eruption of hair on the ears began on the eighth day.

The toes were fused at birth, but from the second or third day on the outer digit on each foot was separated. This was followed by complete separation of all the digits on the fourth or fifth day. In only one case (litter 4) were the toes fused until the sixth day.

The time of incisor eruption was consistent with that noted by MEESTER (1960). Lower incisors appeared one or two days after the uppers, and all incisors were present by the 13th day.

Eyes began to open on the 16th day except in litter 8, in which opening began on the 15th day and litter 9, in which it was delayed until day 18. This was again

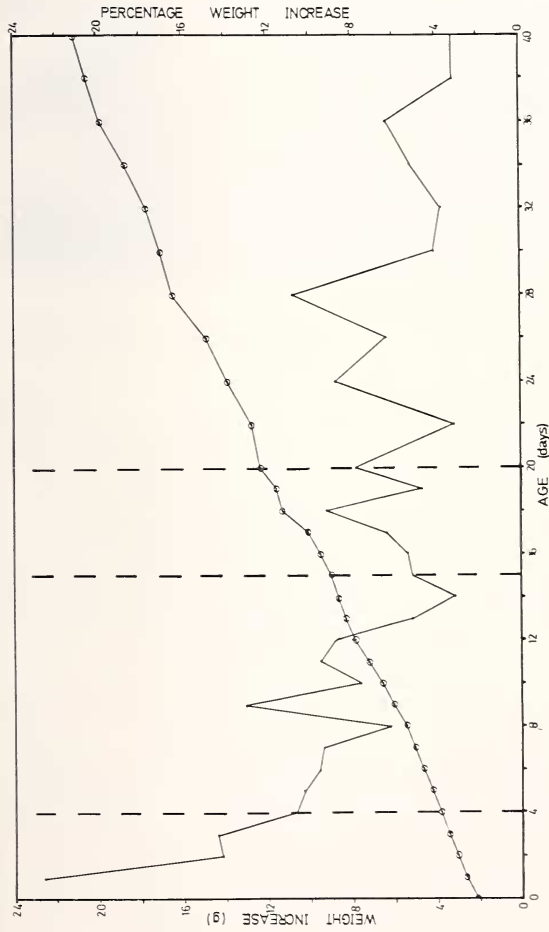
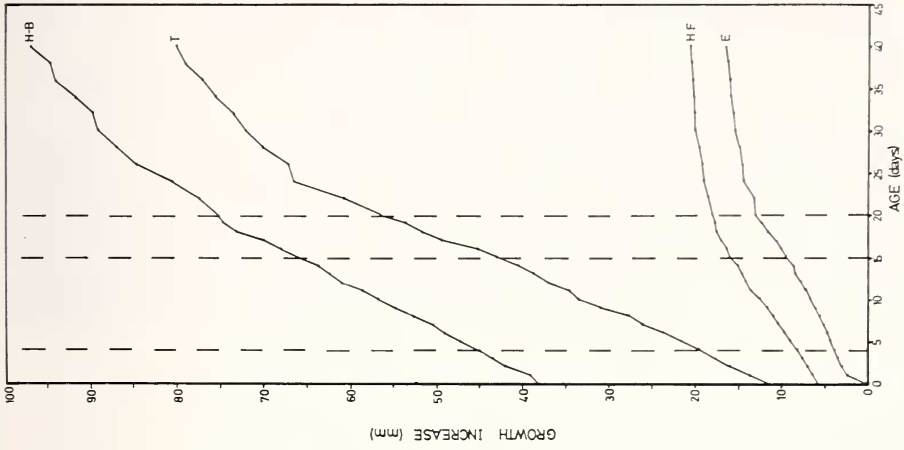


Fig. 1. Mass increase (○) and percentage mass increase of *P. natalensis* from birth until 40 days of age. Vertical broken lines indicate critical periods

Fig. 2 (right). Growth curves of *P. natalensis* from birth until 40 days of age. Vertical broken lines indicate critical periods

consistent with the times noted by MEESTER (1960). Ear pinnae were folded and fused to the sides of the head at birth. Shortly afterwards they opened, but the meatus opened to allow hearing only on the 12th day in most young.

Gonadal development

Ovaries

Until the fifth day the majority of ovarian follicles were primary ones, spherical in shape, and containing a central oogonium. They were separated from the surrounding interstitial tissue by a single layer of follicular cells. In 10-day old animals primary follicles still predominated but some larger central ones had developed. These had a thicker layer of follicular cells and were thus in the first stages of growth. At 15 days this theca folliculi was well developed. By the 20th day the oogonia were surrounded by a well-defined zona pellucida, and could therefore be termed secondary follicles (fig. 3).

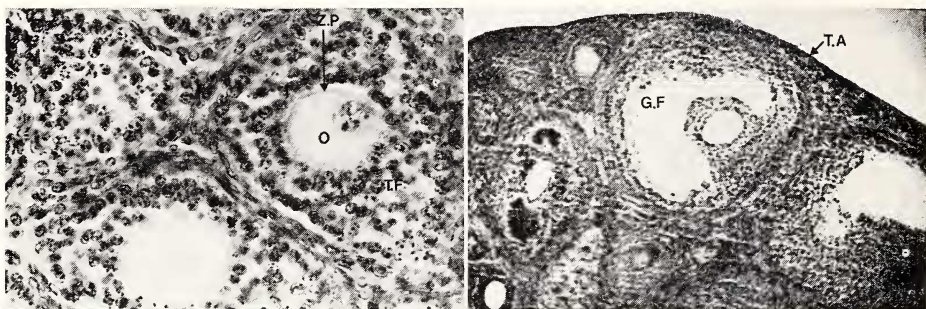


Fig. 3 (left). Section through an ovary of a 20-day old animal showing secondary follicles. T. F — theca folliculi; Z. P — zona pellucida; O — oogonium (X470). — Fig. 4 (right). Section through an ovary of a 40-day old animal showing a Graafian follicle. T. A — tunica albuginea; G. F — Graafian follicle (X115)

In 25-day old animals atretic follicles were noted. This phenomenon may occur at any stage in the development of a particular follicle, and in many cases the oogonium had disintegrated, while the follicular cells had rounded off and floated into the central fluid as small, round, deeply stained particles. Secondary follicles were numerous at this time, and at 30 days had become much enlarged. By the 40th day mature follicles had developed as a result of an accumulation of follicular fluid. A few Graafian follicles were also seen near the margins of the ovaries. No corpora lutea were observed and it was assumed that ovulation had not occurred (fig. 4).

Testes

At five days of age the testes were inactive and seminiferous tubules were clearly delineated by well-formed basement membranes. Little interstitial tissue was present, as at 10 days of age, by which time the tubules contained only spermatogonia adjacent to the basement membrane, gonocytes and supporting tissue (fig. 5).

Some spermatogonia were undergoing mitotic divisions which gave rise to primary spermatozoa in 15-day old animals. Here the number of dividing cells was greater and small lumina had developed in some of the tubule centres. At each stage tubule diameter was noted to increase in size (fig. 7). Little difference was observed between

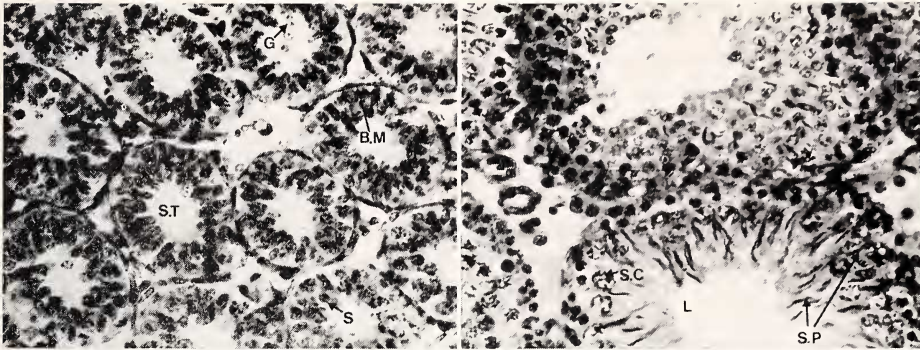


Fig. 5 (left). Section through the testis of a 10-day old animal showing spermatogonia and gonocytes. G — gonocyte; S. T — seminiferous tubule; S — spermatogonium; B. M — basement membrane (X470). — Fig. 6 (right). Section through the testis of a 40-day old animal showing spermatozoa. S. C — primary spermatocyte; S. P — spermatozoa; L — lumen (X470)

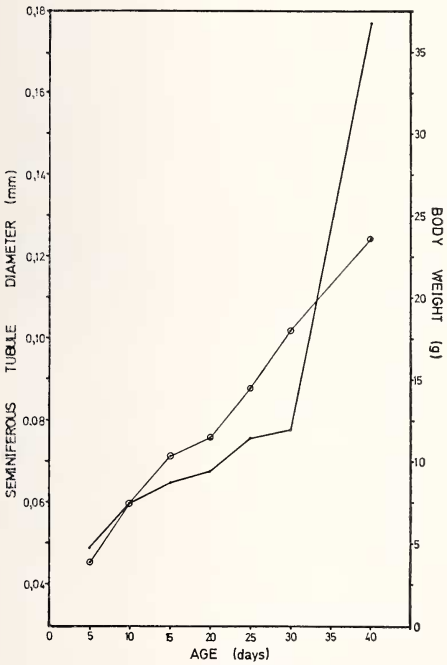


Fig. 7. Body mass (©) and seminiferous tubule diameter in *P. natalensis* from birth until 40 days of age

15- and 20-day old animals, apart from an increase in the amount of interstitial tissue as well as the number of tubules with lumina.

At 25 and 30 days large central gonocytes were observed and the interstitial tissue had continued to build up, indicating that production of spermatozoa would soon occur. Tubule lumina in these sections had also become larger but only in 40-day old animals had spermiogenesis occurred, allowing the formation of spermatozoa from spermatids. Spermatozoa were still attached to Sertoli cells, however, and had not been released into the seminiferous tubule lumina (fig. 6). At this time many spermatogonia were undergoing mitosis and the interstitial tissue had decreased. No sperm were noted in any of the epididymal tubules, thus indicating that productive matings were not possible.

Behavioural development

This is discussed in relation to the natural periods described by WILLIAMS and SCOTT(1953) in house mice. The duration

of these periods is determined by various developments in the growth and maturation of the animals. The periods have therefore been adjusted to allow for differences in rate of development in the two species concerned. The four major stages are: a) neonatal period (0–4 days); b) transition period (5–14 days); c) socialization period (15–20 days); and d) juvenile period (21 days — maturity).

Neonatal period (0-4 days)

This period is defined as that during which development is mainly in growth and strength and in which few overt behaviour patterns develop which are not present at birth (WILLIAMS and SCOTT 1953).

A sense of smell appeared to be present from birth. This was confirmed by small upward and sideways movements of the head, which seemed to be associated with sniffing. The most strongly developed sense during this stage was touch, as shown by the tendency of the young to keep in close contact with one another. Eyes were not open and were seen as dark bulges below the skin surface. Ear pinnae unfolded on the second day in most litters, but hearing was not present.

The young crawled forwards with their hind limbs splayed out on either side of the body. The head, belly and tail were dragged along the ground. The young usually moved in a tight circle, hardly using their hind limbs at all. When stationary they frequently took up a characteristic pose with their limbs tucked in and their heads resting between their forefeet.

At birth the young were unable to right themselves but by the second day most were able to do so by twisting the body and rolling over. However, those of litter 4 only began righting themselves on the third day. The young did not complete the cliff-drop aversion test successfully, and fell off the elevated box. Similarly they were unable to cling to the raised bar during the clinging test. Negative geotaxis was not exhibited and the young remained at the base of the slope with their heads pointing downwards. On the second and third days they began to turn around, trying to face upwards, but were unable to climb due to their inability to grip on to the surface of the slope.

Soft 'puffing' was the only sound made, apart from a very plaintive high-pitched squeak. Puffing occurred with the mouth slightly open and usually in times of stress, such as disturbance of a litter, or during isolation of individual members. When subjected to the various performance tests puffing was prolonged. Because the young were unable to hear at this stage it would seem that puffing served to attract the attention of the parents.

The young suckled to obtain nourishment, and were easily detached from their mothers' nipples. Faeces were eaten by the parents, and elimination often seemed to be induced by the adults licking the ano-genital regions of their young. No self-grooming was noted, except in litter 6 where feeble attempts at scratching were seen. All young were groomed by their parents. Contactual behaviour was present from birth although efforts to maintain contact were limited by the poorly developed motor abilities. Head-waving and short aimless wandering seemed to indicate a need to make contact with other littermates. When isolated the young were unable to make contact with their littermates until the second or third days. This was attributed to their inadequate motor abilities and their inability to sense the presence of their littermates. When they did meet they remained together in a close-pressed group. No aggressive encounters or behaviour were noted, and neither play nor sexual behaviour was observed. On the third day disturbance of a litter in the nest resulted in a 'scatter response', with the young moving quickly and aimlessly in all directions. Mortality was fairly high during this period (see Table) and resulted from killing or accidental squashing of the young by their parents. When they were returned to their cages after observation periods, the parents retrieved them by gripping the loose skin in the dorsal region between their incisors, and carrying them by this.

Transition period (5–14 days)

This period is defined as including the development of hearing, walking and running as well as the appearance of the body fur. It ends immediately before the opening of functional eyes (WILLIAMS and SCOTT 1953).

Although the ear pinnae had unfolded during the neonatal period, the meatus opened only on the 12th day of litters 6, 7, 10 and 11. Response to loud sounds was immediate and was shown by a startle reaction. Sight did not develop but the eye slits became deeper and better formed. Most reactions during this period were therefore controlled by tactile, thermal and olfactory stimuli, as well as by sound in some cases.

Locomotion improved rapidly and this may have been partly attributable to the freed digits. The bellies of the young were still dragged on the ground until approximately the fifth to eighth day. Thereafter the limbs seemed strong enough to support the young animals. Walking was shaky and followed a circular path at first, but by the seventh day movements were less aimless. The tail was dragged along the ground until the 10th to 12th day. Running began at this time but was slow and hesitant at first. Inefficient jumping began on day 13 in litter 3. The righting response was performed immediately the young were placed on their backs. From the eighth day onwards they began to move away from the edge of the elevated box in the cliff-drop aversion test. When placed on the bar in the clinging test, the young were agile enough to attempt to move along it, but often slipped off. Negative geotaxis was exhibited from the sixth day on in most litters, and at the end of this period they climbed unhesitatingly to the top to the slope.

Puffing was still the most frequent sound produced, although it occurred much less often and had usually disappeared by the beginning of the socialization phase. From the seventh day on small, forceful, high-pitched squeaks were made by the young when they were disturbed or handled.

They still obtained their nutrition by suckling and the faeces continued to be eaten by the parents. Most self-grooming involved scratching. On the eighth day the first attempt at face-washing was seen (litter 7), consisting of a feeble motion involving wiping the nose with one forepaw. Overbalancing frequently occurred, especially towards the end of this period, when the young animals attempted to use both forepaws at once. During this activity the anterior part of the body was never lifted far off the ground as in adult grooming behaviour. Occasional attempts were observed at licking the forepaws while face-washing. By the 12th day self-grooming was not yet efficient but was a frequent activity when not sleeping. On the 13th day litters 3, 4, and 11 exhibited mutual grooming which involved licking and nuzzling in the neck and ear regions of littermates. This occurred most frequently when together in the nest.

Efforts to maintain contact with parents and littermates were more productive due to the improved locomotory abilities of the young. On the 10th day the young of litter 8 willingly moved away from their littermates for short periods. This signified the development of an exploratory urge. When isolated the young still strove to make contact with their littermates, and after meeting remained together in a close-pressed group. Aggressive behaviour was still not noted, and neither play nor sexual behaviour seemed to have developed. The scatter response was still present, and when handled the young often jumped vertically into the air. These hops were characteristically associated with a 180° rotation of the body, and a short, sharp squeak. Two or three of these were usually repeated in quick succession. The parents were still very attentive to their young, and continued to retrieve them when they were returned to their cages after observation periods. Mortality was low

and involved only two litters, the young being killed by their parents (litters 6 and 10).

Socialization period (15–20 days)

This period begins with the opening of the eyes and is therefore characterised by the first social interactions between littermates, and by an increase in exploratory behaviour (WILLIAMS and SCOTT 1953). Incisor eruption also occurs.

Hearing was present in all young by this time, and became increasingly acute. Eyes began to open in litter 8 on the 15th day but in litter 9 only on the 18th day. One eye usually opened before the other, but at first the eyes were kept open only when exploring. For the remainder of the time they were kept shut, presumably in order to rest them and to exclude glare. Running was the most common mode of locomotion and had increased in speed and agility. Jumping had begun on the 13th day, and although not very high at first it gradually increased in efficiency. Cliff-drop aversion was well developed and on the 15th day the young began to climb off the elevated box. In the clinging test the young were able, from the 14th day onwards, to walk along the 0.5 cm wide bar without slipping. Immediate negative geotaxis continued to be exhibited. High-pitched squeaks were most frequently produced, but from the 17th day on an occasional deeper and rougher adult-sounding squeak was heard.

On the 17th day the young began to show an interest in solid food by gnawing and smelling at mouse pellets. On the 20th day they were seen to eat and thus weaning was assumed to have occurred. This was voluntary and whatever suckling was observed after this period was not prolonged. (MEESTER 1960, assumed that weaning occurred only when the young had stopped all nursing. In this study weaning was assumed to have occurred as soon as solid food was taken in by the young.) The efficiency of self-grooming increased during this stage and included face, body and tail cleaning. The young began to raise the anterior part of their bodies and could maintain their balance more efficiently.

The young made and maintained contact with one another but exploratory wanderings were more frequent. Because their eyes had opened and hearing had developed they could locate their littermates more easily. After brief encounters they would part to explore their surroundings.

On the 15th day the young of litters 6, 8 and 9 attempted to bite the observer when handled. This was usually accompanied by a low rough squeak. No aggressive encounters between littermates were noted. Play was observed from the beginning of this period. The young ran and jumped skittishly in the observation cage, without provocation and often initiating similar behaviour in the remainder of the litter. No sexual behaviour was noted and testes were not scrotal at this time. Any loud or unusual sound caused immediate dispersal from the nest. Parental grooming was much reduced, probably as a result of increased self-grooming by the young. The members of each family continued to nest together and no deaths were recorded during this phase.

Juvenile period (21 days - maturity)

The behaviour during this period is defined as being essentially adult in nature with the exception of sexual behaviour and care of the young (WILLIAMS and SCOTT 1953).

All sense organs were functioning but the young were initially more agitated by sound and sight stimuli than were their parents. Towards the end of this period their activities settled down into the more unhurried adult pattern. Jumping was efficient and reached a height of approximately 40 cm when the young were 40 days

old. They tended to run rather than walk about, but when disturbed often sat motionless. The rough squeak described in the previous phase was still heard and was louder, but used less frequently. The young ate solid food and drank water, and little if any suckling behaviour occurred. No specific defaecation site was noted. Grooming occurred frequently and included face and body cleaning. Mutual grooming was more prolonged and frequent, but was not commonly observed in mature adults, indicating that this behaviour decreased in frequency after 40 days of age. The young huddled together when sleeping or frightened, but for the rest of the time explored individually or in groups. They never remained isolated for long periods but frequently parted to explore their surroundings.

The young continued to become agitated in the presence of the observer, and attempts to bite when handled were more frequent. From the 35th day onwards tail-rattling was observed. Aggressive encounters between littermates were still not noted, although when an animal was accidentally returned to the wrong cage it was pursued by the inhabitants and threat posture was adopted when encounters occurred. The stranger alternated between escape attempts and short periods of immobility during which its forelimbs were raised over its chest. No attacks were made on the strange animal, however. Similar play activities to those described in the previous phase were observed. On the 26th day some of the chasing noted during play was accompanied by ano-genital nuzzling. In litter 7 attempts at mounting were noted on the 36th day. These were preceded by ano-genital sniffing after which one animal was seen chasing another, with brief attempts at mating when the leading mouse (a female) stopped to rest. This appeared similar to adult mating behaviour. Testes became scrotal on the 26th day in litters 4 and 5.

The young were independent of their parents during this period but nevertheless continued to nest with them. Litters 3, 5 and 10 were produced by the same parents and it was noted that litter 3 attempted to care for the next litter (5) by grooming them and retrieving the members when they were returned to the cage after observation. This was not discouraged by the parents, and no attempt was made by them to oust litter 3 from the nest.

Discussion

Physical development

Percentage mass increase was highest from birth to the first day and, with some fluctuation, decreased from then onwards. This differed slightly from the situation noted by MEESTER (1960) where the percentage increase for the second to the fourth day was highest, followed by a gradual decrease. He explained this in terms of a 'slight set-back which occurs at birth and is made good during the next few days' (MEESTER 1960).

Comparison of mortality rates showed that young conceived in the wild experienced a higher mortality rate i. e. 50%, as opposed to 22.7% amongst young conceived in captivity. Mortality was highest during the neonatal period (Table), and usually resulted from killing by parents. This could be attributed to the fact that the parents had not habituated to their captive condition or to the frequent handling and disturbance of their litters. In only two cases did death occur during the transition period (litters 6 and 10). The young of litter 6 were killed by the mother as they were returned to the cage after the observation period, which would support the suggestion that handling and disturbance of the young may be responsible for their deaths. After the transition period they were capable of avoiding their parents in the event of attempts to injure them.

Litter size and survival of young *P. natalensis*

Litter no.	Mating	Litter size	Survival	
			End of neonatal period	End of transition period
1	Wild	17	0	0
2	Wild	8	3	3
3	Captive	10	6	6
4	Captive	11	8	8
5	Captive	12	12	12
6	Wild	9	9	5
7	Wild	11	6	6
8	Captive	12	12	12
9	Captive	11	10	10
10	Captive	11	11	5
11	Captive	12	8	8
		$\bar{x} = 11.27$		
		SD = 2.28		

Behavioural development

According to SCOTT (1962) there are three major kinds of critical period phenomena:

1. Optimal periods for learning;
2. Optimal periods for infantile stimulation;
3. Optimal periods for the formation of basic social relationships.

These phenomena depend on the development of various physical features. They therefore occur at different stages in the growth of *P. natalensis* and *Mus musculus*, and do not necessarily develop during the same natural periods in the two species.

WILLIAMS and SCOTT (1953) have noted that the neonatal period is a critical one for survival and is characterised by neonatal nutrition i. e. suckling. Deaths that do occur usually result from injuries inflicted by the parents, as noted above. Scattering is an important survival technique, although it is not very well developed at this stage.

It is during the transition period that motor abilities develop rapidly, allowing the young greater contact with their littermates and parents. This is important in that more opportunities for infant stimulation and learning are provided. SCOTT (1962) notes that any strong emotion (hunger, fear, pain or loneliness) speeds up socialization, and during the transition period fear is shown, when the young are disturbed, by their characteristic hops. KING (1958) notes that *Peromyscus maniculatus* shows a similar reaction but only after the development of perceptual awareness of the environment. In *P. natalensis* fear may not facilitate social bonding at this time, because the associated hopping activity is not perceived by littermates and therefore cannot affect them until the socialization phase, when sight develops. Although the young become confident enough to explore on their own by the end of the transition period, their attempts to remain in close contact with their littermates in times of fear indicate that bond formation has begun to develop.

The socialization phase is the most critical one for the formation of basic social relationships. WILLIAMS and SCOTT (1953) note that due to the advance in physical development (sight and hearing) during this phase the young are liable, in natural conditions, to come into contact with strange animals for the first time. This will contribute to the development of social bonds. Voluntary interactions within the

family in the form of mutual grooming, play and agonistic behaviour are probably the most important, allowing the basic social bonds to form.

From the beginning of the juvenile period the young are weaned and are therefore theoretically able to fend for themselves. Nevertheless the high degree of tolerance that *P. natalensis* shows for conspecifics allows large groups of animals to live amicably together. Sibling care was noted in family groups in which a new litter was born while the previous one was still growing up. This, however, included only grooming and attempts at retrieving the young of the second litter. Mutual grooming between siblings of the same litter may play a part in the formation and maintenance of bonds between them.

Sexual behaviour is the most important development during this phase although young *Praomys* have been recorded to give birth from only approximately 77 days onwards (MEESTER 1960). Assuming a minimum gestation period of 23 days (MEESTER 1960), this implies that animals were able to mate successfully from about 54 days. The histological preparations of testes and ovaries confirm this. By 40 days of age no ovulation had occurred in females. In males no sperm were observed in the epididymides, and few in the seminiferous tubules of the testes. Gonadal development appeared to be sufficiently advanced in both sexes to promote sexual behaviour. This did not encompass courtship and true mating by 40 days of age, but was still mainly concerned with exploratory attempts at copulation.

The appearance of these behaviour patterns corresponds with the maturation of the gonads in both sexes, thus suggesting a causal relationship between physiological and behavioural development.

The four natural periods can be regarded as being highly significant in that they reflect critical periods in behavioural development, and particularly development of social behaviour. Although no social relationships are formed during the neonatal period, it is an important one for survival. The transition phase, with its improved locomotory abilities, allows more contact with the immediate family, thus allowing the formation of the first social bonds. Development of sight and hearing during the socialization period are probably the most critical factors leading to the development of social relationships, both within the family and with other strangers that the animal may meet in his natural surroundings. Finally the juvenile phase marks the development of agonistic encounters as well as sexual behaviour. Later on in the life of the animals other critical periods in behavioural development may occur.

Acknowledgements

Thanks are due to Mr. K. B. R. WILLAN for collecting most of the animals studied and to Mr. R. M. BAXTER, for advice on techniques of observation. Particular thanks are due to Mr. L. R. ALEXANDER for assistance and advice concerning the histological aspects of this study. Financial support for this project from the South African Council for Scientific and Industrial Research and the University of Natal Research Committee is gratefully acknowledged.

Summary

The postnatal development of 10 litters of *P. natalensis* was studied from birth until 40 days of age. Litter size, sex ratios and mortality were noted and compared with the findings of MEESTER (1960), as was physical development. Various experimental techniques, as described by BROOKS (1972), were used to follow the development of motor abilities as well as certain behaviour patterns of the young. Parent-offspring relationships concerned with grooming, suckling and juvenile mortality were noted. Histological preparations were made of the gonads of the young at 5, 10, 15, 20, 25, 30 and 40 days of age in an attempt to relate physiological development with the development of sexual behaviour. Behavioural development was recorded during the four natural periods described by WILLIAMS and SCOTT (1953),

i. e. neonatal, transition, socialization and juvenile periods. The duration of these periods was slightly modified to allow for different times of occurrence of the significant developmental changes (WILLIAMS and SCOTT 1953; SCOTT 1962) on which the periods are based. Critical periods of behavioural development were related to these natural periods.

Zusammenfassung

Jugendentwicklung von Praomys (Mastomys) natalensis (A. Smith, 1834)

Die postnatale Entwicklung von *Praomys (Mastomys) natalensis* in Gefangenschaft wurde an 10 Würfen bis zum Alter von 40 Tagen verfolgt. Wurfgröße, Geschlechterverhältnis und Sterblichkeit konnten erfaßt und mit den von MEESTER (1960) gefundenen Werten verglichen werden. Im Weiteren wurde die körperliche Entwicklung beschrieben. Zur Ermittlung der Entwicklung motorischer Fähigkeiten und bestimmter Verhaltensweisen dienten Methoden von BROOKS (1972). Auf die Eltern-Kind-Beziehungen (gegenseitiges Putzen, Säugen, Töten der Jungen) wurde eingegangen. Die Gonadenentwicklung konnte anhand von histologischen Präparaten im Alter von 5, 10, 15, 20, 25, 30 und 40 Tagen verfolgt und mit der Entwicklung des Sexualverhaltens verglichen werden. Die Entwicklung des Verhaltens wurde in vier von WILLIAMS und SCOTT (1953) definierte Perioden gegliedert (Stadium der Neonaten, des Übergangs, der Sozialisation, der Juvenilen) und beschrieben.

References

- BROOKS, P. M. (1972): Post-natal development of the African bush rat, *Aethomys chrysophilus*. Zool. Afr. 7, 85—102.
- JOHNSTON, H. L.; OLIFF, W. D. (1954): The oestrous cycle of female *Rattus (Mastomys) natalensis* (Smith) as observed in the laboratory. Proc. Zool. Soc. Lond. 124, 605—613.
- KING, J. A. (1958): Maternal behaviour and behaviour development in two subspecies of *Peromyscus maniculatus*. J. Mammal. 39, 177—190.
- MAXIMOV, A.; BLOOM, W. (1947): A textbook of histology. Philadelphia, London: W. B. Saunders Co.
- MEESTER, J. (1960): Early post-natal development of multimammate mice *Rattus (Mastomys) natalensis* (A. Smith). Ann. Transv. Mus. 24, 35—52.
- MEESTER, J.; HALLETT, A. F. (1970): Notes on early post-natal development in certain South African Muridae and Cricetidae. J. Mammal. 51, 703—711.
- OLIFF, J. D. (1953): The mortality, fecundity and intrinsic rate of natural increase of the multi-mammate mouse, *Rattus (Mastomys) natalensis* (Smith) in the laboratory. J. Anim. Ecol. 22, 217—226.
- SCOTT, J. P. (1962): Critical periods in behaviour development. Science 138, 949—958.
- TURNER, C. D.; BAGNARA, J. T. (1971): General endocrinology. Philadelphia, London: W. B. Saunders Co.
- WILLIAMS, E.; SCOTT, J. P. (1953): The development of social behaviour in the mouse, in relation to natural periods. Behaviour 6, 35—64.

Authors' address: Miss C. M. BAKER und Dr. J. MEESTER, Department of Zoology, University of Natal, Pietermaritzburg, 3201, South Africa